Coevolution of intelligence, behavioral repertoire, and lifespan

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ABSTRACT

Across many taxa, intriguing positive correlations exist between intelligence (measured by proxy as encephalization), behavioral repertoire size, and lifespan. Here we argue, through a simple theoretical model, that such correlations arise from selection pressures for efficient learning of behavior sequences. We define intelligence operationally as the ability to disregard unrewarding behavior sequences, without trying them out, in the search for rewarding sequences. We show that increasing a species' behavioral repertoire increases the number of rewarding behavior sequences that can be performed, but also the time required to learn such sequences. This trade-off results in an optimal repertoire size that decreases rapidly with increasing sequence length. Behavioral repertoire size can be increased by increasing intelligence or lengthening the lifespan, giving rise to the observed correlations between these traits.

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1. Introduction

The main theoretical question of this paper is how selection for efficient learning shapes the evolution of a species' behavioral repertoire. At first sight, a large behavioral repertoire appears beneficial because it enables an animal to act upon its environment in many ways, thus broadening the spectrum of resources that can be exploited. A crab's claws, for example, can just grasp and crush, while the hands of primates can perform a large range of manipulations that contribute to impressive feeding behavior (Strier, 2010). Why, then, do not all species have large behavioral repertoires? Apart from constraints on the evolution of morphology and motor control (Arnold, 1992), we argue that a large repertoire incurs a hidden cost because it increases the time necessary to learn functional sequences of behaviors. Our argument rests upon two observations. First, behavioral repertoires are mainly genetically determined and are often limited to a small number of behaviors. Second, animals obtain rewards by combining these genetically determined behaviors into learned sequences (we use the term "reward" to indicate any positive contribution to fitness, such as food, shelter, safety from predators, temperature regulation, and so on).

All species have an inborn repertoire of behavior patterns that develop without any specific experiences (Hinde, 1970; Hogan, 2001; Berridge, 1994; Lorenz, 1981). These patterns, called *fixed action patterns* in ethology, are centrally generated and are typically performed by young animals without peripheral or external feedback (Hinde, 1970; Hogan, 2001; Lorenz, 1981). Rat pups, for example, can suckle from birth without any need for learning (Hall et al., 1975). Similarly, movements used in dust bathing in chickens develop spontaneously during the first two weeks of life, before they are used in dust bathing (Larsen et al., 2000; Vestergaard et al., 1990). Ethologists have determined the inborn behavioral repertoire of many species and studied its evolution and genetic determination through comparative methods (Hinde and Tinbergen, 1958; Lorenz, 1981, 1941) and the observation of species hybrids (see Dilger, 1960, Buckley, 1969 for the selection of nest material in parrots, and Lingle, 1993, Lingle, 1992 for gait in deer). Of greatest relevance to this paper are studies about exploratory behavior and learning. Glickman and Sroges (1966) assessed exploration of novel objects in more than 100 mammal and reptile species, reporting great variation in the quantity and form of exploratory behavior. Primates and carnivores explored the most, followed by rodents, marsupials, insectivores and edentates; reptiles explored the least. Time spent exploring correlated with the number of exploratory behaviors. Rodents, for example, mainly sniffed and gnawed at novel objects, while many primates engaged in extensive manipulation and prolonged visual inspection. Consistent species differences in exploratory behavior have also been reported in foraging behavior (Mettke-Hofmann et al., 2002), including differences in how experience influences future exploration (Mettke-Hofmann and Gwinner, 2003).

Ethologists have also demonstrated that individual experience is important to organize inborn behaviors into functional sequences. A squirrel (*Sciurus vulgaris*), for example, uses several behaviors to open a nut, such as holding, gnawing, and prying (Eibl Eibesfeldt, 1975). Young squirrels can hold, gnaw, and pry, but

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are inefficient nut openers because they use these behaviors randomly on the surface of the nut, until it cracks. By trial and error, they gradually learn how to assemble these behaviors into an efficient sequence (Eibl Eibesfeldt, 1963, replicated in *S. lis* by Tamura, 2011). This example brings us to our second observation, and the crux of our argument. Learning, to contribute substantially to individual fitness, should not be limited to the acquisition of single behaviors in response to specific stimuli. Rather, fitness is most enhanced when coordinated sequences of behaviors are acquired. Learning sequences is much harder than learning single responses because of a combinatorial explosion in the number of sequences that can be tried out. The development of tool use in chimpanzees (*Pan* troglodytes) exemplifies this problem. Inoue-Nakamura and Matsuzawa (1997) studied how chimpanzees at Bossou, Guinea, learn to crack nuts with stone or wooden anvils and hammers, using a sequence of five behaviors: pick up a nut, place it on the anvil, pick up a hammer (requires a different grip than picking up a nut), hit the nut, and eat the nut. It takes the chimpanzees thousands of attempts over three or more years to learn this sequence. Apart from perfecting the necessary motor skills, we argue that a major difficulty in such learning is that the five actions must be chosen among many. Inoue-Nakamura and Matsuzawa (1997) observed the animals perform at least 35 different actions on stones and nuts. Chimpanzees can thus potentially perform at least $35^5 \simeq 50$ million sequences of 5 behaviors involving stones and nuts. How to find the correct sequence among so many? There are at least two different ways, not mutually exclusively, to resolve this combinatorial dilemma and reduce sequence learning times.

1. Limiting the behavioral repertoire. If chimpanzees could only perform on stones and nuts the 5 actions they actually need to open the nuts, they would only need to try $5^5 = 3125$ sequences. This would, of course, limit what they can do in other situations.
2. Intelligence. We define intelligence as the ability to disregard, without explicitly trying them out, behavior sequences that are not profitable (this definition includes both individual and social learning, see Section 4). Chimpanzees could, for example, understand that placing the nut on the anvil is the first thing to do. This would reduce the number of sequences to try to $35^4 \simeq$ 1.5 million. If chimpanzees further understood that picking up the hammer should come next, the number of sequences to try would decrease to $35^3 \simeq 40,000$.

In the following, we introduce a simple mathematical model to study the coevolution of behavioral repertoire and intelligence under the selection pressure for efficient learning of functional sequences of behavior. The model predicts that large behavioral repertoires should be observed only in intelligent and long-lived species. We evaluate this prediction in a concluding Discussion.

2. The model

We introduce a model environment and a model animal that learns from interacting with the environment, and then calculate the optimal repertoire size for the animal. The environment is described by the following assumptions:

1. There are A actions that can be used to act upon the environment (e.g., grasp, push, pull, lift, twist, and so on). An animal's behavioral repertoire may comprise any number of actions between 0 and A.
2. The environment delivers a reward of 1 to the animal each time a specific sequence of l actions is performed. Other sequences yield zero reward—this is actually a cost because the time spent performing an unrewarding sequence could have been spent earning a reward.

3. Each action has the same probability to be part of the rewarding sequence. That is, the probability that an action is the correct one at any point in the sequence is $1/A$.
4. The rewarding sequence does not change over an animal's lifetime.

We make the following assumptions about animal behavior:

5. The behavioral repertoire is genetically determined, but the animal must learn which actions to use to obtain rewards.
6. The animal can perform a total of T actions in its expected lifetime (all actions take the same time).
7. The animal explores the environment by performing sequences of l actions at random until it stumbles upon the rewarding sequence and collects a reward. Thereafter, the animal continues to perform the rewarding sequence until it dies.
8. Actions can be added freely to the behavioral repertoire (there are no morphological or genetic constraints).

These assumptions are clearly a simplification of actual learning strategies. Animals, for example, usually take more than one experience to learn. They also do not try actions randomly, but use a variety of mechanisms to explore the environment in a more targeted way. Our model environment is also highly simplified. In a realistic environment some behaviors may have a higher probability of entering profitable sequences (a departure from assumption 3), and in general there are many profitable sequences which differ in length and value (a departure from assumption 2). After discussing this simple model, we will show how to generalize it to different learning strategies and more realistic environments.

3. Evolution of repertoire size

We want to calculate the reward, $r_l(n)$, that an organism with a repertoire of n behaviors expects to collect under the hypotheses above, when attempting to learn a sequence of length l. Conditioning on the probability that the repertoire contains all l actions required to collect a reward, we write

$$
\begin{aligned}
r_l(n) &= \text{E(reward)} \\
&= \text{E(reward | all actions in repertoire)} \\
&\quad \times \text{Pr(all actions in repertoire).}
\end{aligned} \tag{1}
$$

The first term is the number of times the animal is expected to complete the profitable sequence. If the animal devoted all of the available T actions to performing the rewarding sequence, it would collect $\lfloor T/l \rfloor$ rewards ($\lfloor x \rfloor$ is the integer part of x). Some of the T actions, however, are used to learn, i.e., to search for the rewarding sequence among all possible sequences. We can thus write

$$
\text{E(reward | all actions in repertoire)}
$$
$$
= \left(\left\lfloor \frac{T}{l} \right\rfloor - \text{sequence search time} + 1 \right). \tag{2}
$$

where we add 1 because the learning phase terminates with a successful performance of the rewarding sequence. The sequence search time is calculated based on assumptions 5–7 as follows. With a repertoire of n actions, the animal can try out n^l sequences of length l. Each such attempt requires l time steps. If sequences are tried out at random, with no memory of what has been tried before, the expected time to find the profitable sequence is

$$
\text{sequence search time} = ln^l \tag{3}
$$

resulting in

$$
\text{E(reward | all actions in repertoire)} = \left(\left\lfloor \frac{T}{l} \right\rfloor - ln^l + 1 \right). \tag{4}
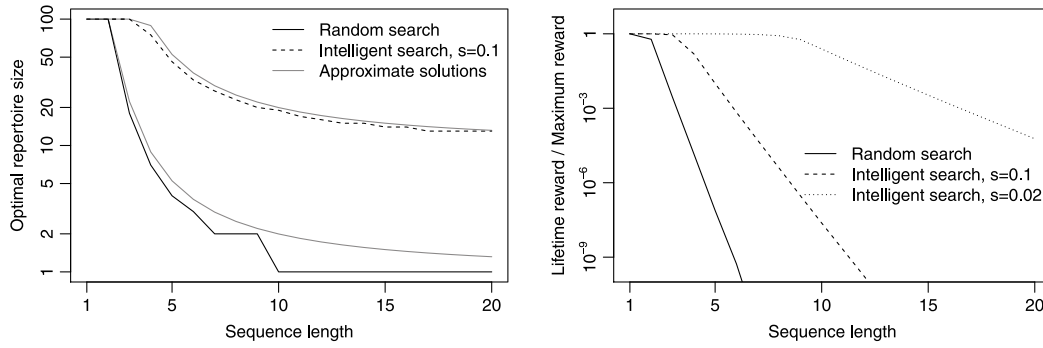$$

Fig. 1. Left: optimal repertoire size vs. sequence length for random search and intelligent search of rewarding action sequences (see text). Approximate solutions are calculated according to Eqs. (7) and (9). Right: lifetime reward vs. sequence length, when using behavioral repertoires of optimal size. Lifetime reward is expressed as a proportion of its maximum value $\lfloor L/l \rfloor$, corresponding to an organism with a full behavioral repertoire ($n = A$) and innate knowledge of the rewarding sequence. Lifetime reward decreases rapidly with sequence length, but intelligence can overcome such a decrease up to a certain sequence length. Model parameters: $T = 10^5$, $A = 100$.

The second term in Eq. (1) can be calculated in two ways. The first is to assume that the organism's repertoire of n different actions is built first, and then ask what is the probability that, when building a sequence of l actions, we choose only actions that have been included in the repertoire. The second way is to assume that the rewarding sequence is built first, and then ask what is the probability that a random choice of n actions includes all actions in the sequence. The two ways are equivalent because the repertoire and the rewarding sequence are built independently of each other. The first way results in simpler calculations and is pursued below. The second way is presented in Appendix A.

The organism's behavioral repertoire is a random sample of n different actions out of A possible ones. The rewarding sequence is constructed by randomly selecting l actions out of A. In terms of probabilities, this is equivalent to having A boxes, of which n are marked, placing l balls randomly in one of the boxes, and asking the probability that all boxes receiving a ball are marked. The probability that a ball is placed in one of the marked boxes is n/A. Because the l balls are placed independently of each other, the probability that they are all placed in marked boxes is the product of the probabilities for placing each ball in a marked box, resulting in

$$\Pr(\text{all actions in repertoire}) = \left(\frac{n}{A}\right)^l. \tag{5}$$

Given Eqs. (4) and (5), the expected reward in Eq. (1) becomes

$$r_l(n) = \frac{n^l}{A^l}\left(\left\lfloor \frac{T}{l} \right\rfloor + 1 - ln^l\right). \tag{6}$$

The value of n that maximizes this expression is the optimal repertoire size. Note that the number of possible actions, A, enters only through a multiplicative factor and thus does not influences repertoire size other than constraining it to $n \le A$.

The first term in Eq. (6) increases monotonically (a larger repertoire is more likely to contain all necessary actions), while the second term decreases monotonically (it takes more time to try out sequences composed of more actions). We show in Appendix B that Eq. (6) has exactly one maximum in n (provided T/l is not too small), which is thus the optimal repertoire size. Fig. 1 (right panel, solid line) shows that a large behavioral repertoire (up to a limit of $n = A$) is optimal for very short sequences. As sequence length increases, however, repertoire size drops rapidly. We can gain insight into this result by noting that the expected reward in Eq. (6) vanishes for large enough n. Hence an upper bound for repertoire size is given by the solution of $r_l(n) = 0$, or

$$\hat{n}_l = \sqrt[l]{\frac{1}{l}\left(1 + \left\lfloor \frac{T}{l} \right\rfloor\right)} \simeq \sqrt[l]{\frac{T}{l^2}} \tag{7}$$

where, for simplicity, we discarded the 1 addend and the $\lfloor \cdot \rfloor$ function. The value in Eq. (7) is an excellent approximation of the optimal behavioral repertoire size (Fig. 1, gray lines), because as repertoire size increases the second factor in Eq. (6) decreases toward zero very rapidly (note that $\hat{n}_l = A$ should be used if Eq. (7) exceeds A).

4. Evolution of intelligence

So far, we have assumed that animals try actions at random until they stumble upon the rewarding sequence. More efficient search strategies are, of course, possible. The key observation to model such strategies is that, regardless of details, a strategy confers an evolutionary advantage only to the extent that it shortens the time to find rewarding behavior sequences. In other words, intelligence can be defined as the ability to disregard unrewarding behavior sequences without trying them out. Here we choose the simplest way to model this effect in order to demonstrate how intelligence influences behavior repertoire (other models are possible, see below). Namely, we introduce an "intelligence" parameter, $s < 1$ such that, at each step in a sequence, the number of behaviors to consider is reduced by a factor s (smaller values of s indicate larger intelligence). Including such a factor in Eq. (6) yields

$$r_l(n) = \frac{n^l}{A^l}\left(\left\lfloor \frac{T}{l} \right\rfloor + 1 - ls^l n^l\right), \tag{8}$$

which leads to a simple modification of Eq. (7):

$$\hat{n}_l \simeq \frac{1}{s}\sqrt[l]{\frac{T}{l^2}}, \tag{9}$$

or, taking logarithms

$$\log \hat{n}_l = \log \frac{1}{s} + \frac{1}{l}\log T - \frac{2}{l}\log l. \tag{10}$$

These equations imply that behavioral repertoire should increase, compared to Eq. (7), in proportion to the ability to disregard unrewarding sequences. This ability can be realized in a number of ways, not mutually exclusive. One such way is through genetic predispositions to use behaviors in specific contexts. For example, swallowing is useful when foraging but not, usually, when courting. This strategy partitions the behavioral repertoire into smaller subsets (possibly overlapping) which, in any given context, result in shorter search times. There is ample evidence for context dependent repertoires (or "behavior systems"; see Breland and Breland, 1961, Hogan, 1994 and Hogan, 2001). For example, rats tend to move away from stimuli that signal shock, and learn only with great difficulty if they have to approach a stimulus (or press a lever)

in order to avoid shock (Bolles, 1970). The examples recalled in the introduction, about squirrels and chimpanzees learning to open nuts, clearly demonstrate how context dependent repertoires facilitate learning. Both species, when foraging, try out behaviors that appear more likely to be productive, and avoid behaviors such as vocalizing or courting that would in all likelihood be unproductive in a foraging context.

Stimulus generalization is another ability that facilitates learning. An animal that has learned that a response to a stimulus is rewarded (unrewarded) will tend to respond (not respond) also to similar stimuli (Mackintosh, 1974; Ghirlanda and Enquist, 2003). To the extent that similar stimuli signal similar environmental states, stimulus generalization enables animals to try out behaviors that have a higher probability of leading to reward, and to avoid those that are likely unrewarding. The list of abilities that has been suggested to underlie animal learning and behavior is long, and includes conditioned reinforcement, cognitive maps, planning, inference, social learning, and so on (Bouton, 2007; Pearce, 2008). The evolution of these abilities is beyond our present scope, but we note that they can all be modeled, for the present purposes, as shortening the time it takes to discover functional behavior sequences.

5. Model generalization

In this section we show that the main conclusions derived above for a very simple environment also apply to more realistic ones. We have assumed so far a stationary environment (assumption 4), but it is easy to see that environmental variability can only reduce repertoire size, compared to a constant environment. In a variable environment, in fact, a behavior sequence can stop being rewarding, requiring the animal to learn a new sequence. Thus environmental variability increases search times, thereby reducing optimal repertoire size (Eq. (2)). We have also assumed that all behaviors are equally likely to enter a profitable sequence (assumption 3). The upper bound to behavioral repertoire size in Eq. (7), however, holds also when some behaviors are more likely than others to enter rewarding sequences. The reason is that (7) depends only on the vanishing of the first factor in Eq. (1), while the probabilities of behaviors being part of the rewarding sequence only appear in the second factor (the expression $(n/A)^l$ would be replaced by $(\sum_{i=1}^{n} p_i)^l$, where p_i is the probability that the i-th behavior in the repertoire enters the rewarding sequence). Of course, in this case behavioral repertoires would be under selection to include the more useful behaviors at the possible exclusion of less useful ones.

A seemingly restrictive assumption is the existence of a single rewarded sequence in the environment (assumption 2). Many rewarding sequences exist in real environments, differing in both length and reward. Under such conditions, a learning strategy must also determine how much time to spend searching for sequences of different length. We show in Appendix C that natural selection favors searching for sequences of a given length, using a behavioral repertoire of the appropriate size for that length, as determined above. Thus our previous conclusion, that large repertoire sizes should be observed only in species with long lifespan and high intelligence, also holds for environments with a varied distribution of rewards. Another line of reasoning leads to the same conclusion. We have assumed above that animals look for sequences of a fixed length l, which matches the length of the rewarding sequence (assumption 7). In addition to the theoretical argument just given, two general findings about learning justify this assumption. First, learning mechanisms operate within well-defined, typically short time spans. For example, instrumental learning in rats and pigeons becomes almost impossible if the animal is required to remember stimuli for more than one or two minutes (Nelson

and Wasserman, 1978; Roper, 1983). This imposes an upper bound on the length of sequences that can be learned. Second, artificial selection experiments show that exploratory drive is under robust genetic control (Dingemanse and Réale, 2005). Tryon (1940), for example, significantly altered rat exploratory behavior in just seven generations. Thus we expect natural selection to tailor exploratory drive to a species' needs. These findings further support the idea that animals look predominantly for sequences of behavior whose length matches their learning ability and lifespan.

6. Discussion

Our results suggest that intelligence, behavioral repertoire, and lifespan co-evolve under the selection pressure for efficient learning of functional behavior sequences. Specifically, increasing lifespan and decreasing sequence search time (increasing "intelligence") are two ways in which an individual can perform more rewarding sequences in a lifetime, paving the way for the evolution of larger behavioral repertoires. Empirical data, although by no means comprehensive, appear to support this coevolutionary scenario. Changizi (2003) shows that mammalian behavioral repertoires scale as a power of encephalization, which is consistent with Eq. (10) if we assume that encephalization is itself related to intelligence by a power law (recall that "intelligence" is quantified by $1/s$ in Eqs. (8)–(10)). Eq. (10) also predicts that behavioral repertoire should correlate with lifespan. We could not assess this correlation directly. Data on encephalization and lifespan are reported in Hofman (1984, 1993) and Allman et al. (1993), but include only a few of the species for which Changizi (2003) provides estimates of repertoire size. A positive correlation exists between lifespan and encephalization, as predicted both by our model (as lifespan and encephalization are subject to similar selection pressures and both contribute to large repertoire size) and by arguments based on brain–body physiological interactions (Hofman, 1993; Allman, 1999). A larger data set, containing information on behavioral repertoire, lifespan, and encephalization for many species, is required for a fuller test of our results.

Our model also has consequences for understanding comparative cognition. Exploratory behavior (including play) can influence both motor development (e.g., Nunes et al., 2004) and problem solving (e.g., Benson Amram and Holekamp, 2012). Thus, to understand species differences in intelligence, it might prove fruitful to study variation in behavioral repertoire size and aspects of exploration such as exploratory drive and duration of juvenile periods (during which most learning occurs), in addition to investigating cognitive mechanisms.

Appendix A. Alternative proof of Eq. (5)

To illustrate an alternative way of proving Eq. (5) we start with the case of sequences of length $l = 2$. We imagine a sequence of two actions is built first, and then we ask what is the probability that the organism's repertoire contains all actions in the sequence. Constructing a sequence of length 2 can result in choosing twice the same action (case 1) or in choosing two different actions (case 2). The two cases are mutually exclusive hence their probabilities sum.

Case 1 occurs with probability A/A^2, since there are A possible ways of choosing the same action twice and A^2 possible choices of two actions (writing A/A^2 rather than $1/A$ helps to see a pattern later). In this case, the probability that the n different actions in the organism's repertoire include the single selected action is n/A. Case 2 occurs with probability $A(A - 1)/A^2$ (there are $A(A - 1)$ ways of choosing two different actions and A^2 possible choices of two actions). In this case, the probability that the repertoire has both actions is $\frac{n}{A}\frac{n-1}{A-1}$ (for the first action, one of n actions in the

repertoire must match one of A possible actions; for the second action, one of the remaining $n - 1$ actions must match one of $A - 1$ possible actions—not A because in case 2 the sequence is composed of different actions). Thus the probability that the repertoire has the two actions necessary to complete the sequence is

Pr(two actions in repertoire)

$$= \frac{1}{A} \times \frac{n}{A} + \frac{A(A-1)}{A^2} \times \frac{n}{A} \frac{n-1}{A-1}$$

$$= \frac{n}{A^2} + \frac{n(n-1)}{A^2} = \frac{n^2}{A^2} \tag{A.1}$$

which is the same as Eq. (5) for $l = 2$. The reasoning can be extended to sequences of length $l > 2$ as follows. The probability that selecting l actions out of A results in k different actions is

$$\text{Pr}(k \text{ different actions}) = \frac{1}{A^l} \left\{ \begin{matrix} l \\ k \end{matrix} \right\} \prod_{i=0}^{k-1} (A - i) \tag{A.2}$$

where $\left\{ \begin{smallmatrix} l \\ k \end{smallmatrix} \right\}$ is the number of ways in which l actions can be distributed among k specific actions, and the product in Eq. (A.2) arises because there are A ways of choosing the first of the k actions, $A - 1$ ways of choosing the second, and so on. $\left\{ \begin{smallmatrix} l \\ k \end{smallmatrix} \right\}$ is known as a Stirling number of the second kind: it is the number of ways in which a set of l elements can be partitioned into k non-empty sets, or the number of ways in which l balls can be put into k boxes without leaving any box empty (Graham et al., 1989). Note that the identity $\sum_{k=1}^{l} \text{Pr}(k \text{ different actions}) = 1$ implies

$$\sum_{k=1}^{l} \left\{ \begin{matrix} l \\ k \end{matrix} \right\} \prod_{i=0}^{k-1} (A - i) = A^l, \tag{A.3}$$

a fact that we will use later. The probability that repertoire of n different actions contains k specific actions ($k \leq n$) is

$$\text{Pr}(\text{repertoire has } k \text{ actions}) = \prod_{i=0}^{k-1} \frac{n - i}{A - i}, \tag{A.4}$$

see the case $l = 2$ above. Thus we have

Pr(l actions in repertoire)

$$= \sum_{k=1}^{l} \text{Pr}(k \text{ different actions})$$

$$\quad \times \text{Pr}(\text{repertoire has } k \text{ actions}) \tag{A.5}$$

$$= \sum_{k=1}^{l} \frac{1}{A^l} \left\{ \begin{matrix} l \\ k \end{matrix} \right\} \prod_{i=0}^{k-1} (A - i) \prod_{i=0}^{k-1} \frac{n - i}{A - i} \tag{A.6}$$

$$= \frac{1}{A^l} \sum_{k=1}^{l} \left\{ \begin{matrix} l \\ k \end{matrix} \right\} \prod_{i=0}^{k-1} (n - i). \tag{A.7}$$

Using Eq. (A.3), we obtain that the sum is n^l, resulting in Eq. (5) in the main text. As an example, for $l = 3$ we have

Pr(3 actions in repertoire)

$$= \frac{1}{A^3} \sum_{k=1}^{3} \left\{ \begin{matrix} 3 \\ k \end{matrix} \right\} \prod_{i=0}^{k-1} (n - i) \tag{A.8}$$

$$= \frac{1}{A^3} \left[\left\{ \begin{matrix} 3 \\ 1 \end{matrix} \right\} n + \left\{ \begin{matrix} 3 \\ 2 \end{matrix} \right\} n(n - 1) \right.$$

$$\left. + \left\{ \begin{matrix} 3 \\ 3 \end{matrix} \right\} n(n - 1)(n - 2) \right] \tag{A.9}$$

$$= \frac{1}{A^3} [n + 3n(n - 1) + n(n - 1)(n - 2)] \tag{A.10}$$

$$= \frac{n^3}{A^3}. \tag{A.11}$$

Appendix B. Existence and uniqueness of optimal repertoire size

Here we prove that $r_l(n)$ in Eq. (1) has a unique maximum. For this purpose, n can be considered as a continuous variable ($n \geq 1$). We define

$$f_l(n) = \left(\frac{n}{A} \right)^l \qquad g_l(n) = \left\lfloor \frac{T}{l} \right\rfloor + 1 - ln^l$$

so that $r_l(n) = f_l(n)g_l(n)$. We note that $f_l(n)$ is monotonically increasing in n while $g_l(n)$ is monotonically decreasing. Let $\bar{n}$ be the zero of $g_l(n)$, $\bar{n} = \sqrt[l]{(\lfloor T/l \rfloor + 1)/l}$. We have

$$f_l(1) = 1/A^l \qquad f_l(\bar{n}) = (\bar{n}/A)^l$$
$$g_l(1) = \lfloor T/l \rfloor + 1 - l \qquad g_l(\bar{n}) = 0. \tag{B.1}$$

We also have

$$f'_l(n) = ln^{l-1}/A^l \qquad f'_l(1) = l/A^l \qquad f'_l(\bar{n}) = l\bar{n}^{l-1}/A^l$$
$$g'_l(n) = -l^2 n^{l-1} \qquad g'_l(1) = -l^2 \qquad g'_l(\bar{n}) = -l^2 \bar{n}^{l-1} \tag{B.2}$$

and

$$r'_l(n) = f_l(n)g'_l(n) + f'_l(n)g_l(n). \tag{B.3}$$

The existence of at least one maximum in $[1, \bar{n}]$ derives from the fact that $r_l(n)$ is continuous and that, according to Eqs. (B.1) and (B.2), it is positive and increasing at $n = 1$ while it is zero and decreasing at $\bar{n}$. The uniqueness of the maximum derives from the fact that, according to Eq. (B.3), the maximum satisfies

$$\frac{f_l(n)}{g_l(n)} = -\frac{f'_l(n)}{g'_l(n)}. \tag{B.4}$$

The l.h.s increases in $[1, \bar{n}]$ from a positive value of $f_l(1)/g_l(1) = 1/\left(A^l(\lfloor T/l \rfloor + 1 - l) \right)$ to infinity, while the r.h.s. is constant at $-f'_l(n)/g'_l(n) = 1/lA^l$, which is higher than the previous value if $T \gg l$. Thus the two sides of Eq. (B.4) equal each other only once.

Appendix C. Extension to general environments

Let q_l be the frequency of rewarding sequences of length l, R_l the expected reward, and u_l the fraction of the available time that the animal allocates to sequences of length l. A straightforward extension of the reasoning above shows that the quantity to be maximized to find the optimal repertoire size is now

$$r = \sum_{l=1}^{l_{\max}} q_l R_l \frac{n^l}{A^l} \left(\left\lfloor \frac{u_l T}{l} \right\rfloor + 1 - ls^l n^l \right)$$

$$= \sum_{l=1}^{l_{\max}} q_l R_l r_l(n, u_l),$$

where $l_{\max}$ is the maximum sequence length, $\sum_{l=1}^{l_{\max}} u_l = 1$, and $r_l(n, u_l)$ is defined as $r_l(n)$ in Eq. (8), but with a reduced number of actions, $u_l T$. Clearly the optimal strategy is to focus on sequences of length such that $q_l R_l r_l(n_l^\star, 1)$ is maximized ($n_l^\star$ is the optimal behavioral repertoire for sequences of length l and unitary reward, i.e., the solution of Eq. (6)). Any departure from such strategy, in fact, would devote part of the animal's time to sequences with lower rewards. (Also note that longer sequences must carry exponentially larger reward to be profitable, because the reward that can be gained in a lifetime is an exponentially decreasing function of sequence length, see Fig. 1, right, and Eq. (1).)

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